

hensively referenced, and in view of the typical production times of multicontributor works, the references are remarkably up to date. Many are from 1994 with one or two as late as 1995. Nevertheless, the missing references in chapter 6 remain an irritating oversight.

The editors contend that this book should appeal to a diverse readership and I think they are correct. It should serve as a valuable reference text, both for professional scientists and engineers and for the advanced student of limnology, although cost may be an issue in the latter case. I enjoyed reading it and it will make a welcome addition to my bookshelf.

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ANDERSEN, T. 1997. **Pelagic nutrient cycles: Herbivores as sources and sinks.** Ecological Studies, V. 129. Springer, Berlin. ISBN 3-540-61881-3. 280 p. \$79.95.

What if there were something of critical importance to nutrient cycling and trophic dynamics, something unarguably fundamental to biological reality, something that had been *right in front our eyes*, but that had somehow been overlooked by ecologists? Such a situation seems almost impossible given the explosive growth of ecology over the past half century. Nevertheless, the new book by Norwegian limnologist Tom Andersen, *Pelagic Nutrient Cycles: Herbivores as Sources and Sinks*, formalizes the major consequences of a simple realization that has been dawning on a number of aquatic scientists over the past decade. That realization, put bluntly, is that animals are not made of pure energy (or pure phosphorus, for that matter). Instead, animals are constructed of multiple chemical elements (C, N, P, others) and to grow maximally must satisfy not only their energetic requirements for growth and maintenance but also their somatic requirements for major elements and biomolecules. (Reader alert! The author of this review has slowly arrived at this realization himself via various means and thus was predisposed to like this book.) Recent years have seen a flurry of laboratory and field studies examining various ramifications of this simple insight, from laboratory food quality assessments to field determinations of the stoichiometry of consumer-driven nutrient recycling. However, as noted by Robert MacArthur and quoted in chapter 1, "Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true . . . that it is best not to put too much faith in facts until they have been confirmed by theory." For aquatic scientists who have not yet brought themselves to trust the stoichiometric "facts" arrayed to date, here, in Andersen's brilliant book, is the theory.

The book, #129 in Springer's Ecological Studies series, is a direct transcription of Andersen's Ph.D. thesis at the University of Oslo (under the direction of E. Paasche). The writing is extremely clear and well edited. The book starts big (with an emphasis on P loading and the eutrophication problem; chapters 1–2) and ends big (connecting food webs with eutrophication; chapters 5–7) and in between moves methodologically through a mechanistic treatment of algal growth and nutrition, zooplankton growth and nutrition, and their reciprocal interactions via nutrient recycling. The theory development builds on sound physiological principles for both algae (chapter 3) and grazers (chapter 4), systematically considers size- and age-dependent grazer population models (chapter 4), and eventually leads to a synthetic treatment of the dynamic interactions

among nutrients, algae, and grazers (chapter 5), adding bacteria in chapter 6. The model structure might be referred to as "stoichiometrically explicit." Let me explain. Ecology made a major advance with the development of "spatially explicit" ecological models that incorporate the constraints that space and rates of movement through space place on ecological dynamics. Similarly, a stoichiometrically explicit model captures the constraints that matter and energy (both!) place on ecological dynamics. As pointed out by Andersen, a number of influential models of nutrient cycling in food webs ignore such constraints and contain assumptions and formulations that generate model conditions that do damage to the first law of thermodynamics (e.g. grazers apparently synthesizing new P atoms within their bodies!).

In Andersen's model such absurd situations are impossible. The system of equations incorporates three key aspects of the stoichiometry of any autotroph-grazer-nutrient system. First, algal elemental composition (in terms of C:P ratio) is variable with algal nutritional state and scales with P supply rate and algal demand. Second, zooplankton grow maximally when both their energetic and somatic nutritional needs are met, with lower growth rates when food quantity is low but also when food quality is low and the animals are unable to meet their body P requirements. Third, release of limiting nutrient P is constrained by mass balance as the difference between ingested P and that incorporated into new biomass. Thus, there is a system of potentially complex interactions between P supply rate, algal growth rate and C:P ratio, and zooplankton growth and release of P. To my knowledge this is the first fully dynamic theory of trophic dynamics and nutrient cycling to include these three key realities.

What are the consequences of formalizing these biologically realistic assumptions? What happens when the wildly variable elemental composition of autotrophs interacts with the rigidly regulated, but species-specific, requirements of consumers? Andersen shows that the results are dramatic. In this system of equations, depending on model parameters, a limiting nutrient conceivably can cycle rapidly amongst dissolved, algal, and grazer pools, supporting high production with grazers as a key "source" of limiting nutrient, or spin off into a deteriorating syndrome in which P-limited algae develop high C:P ratios that induce slow, P-limited grazer growth with reduced P release rates (grazers are now a major "sink" of P), further accentuating algal P limitation. In other words, introducing stoichiometric reality to the interaction generates bifurcations in system behavior, bifurcations that are absent from single currency models. Chapter 6 ("Approaching Planktonic Food Webs: Competition, Coexistence, and Chaos") illustrates how complex indeed these interactions can become. While limitations of computer technology at the time that Andersen completed this work prevented him from formally assessing whether this system of equations generates true deterministic chaos, examination of the model output in this chapter leads a nonmathematician such as myself to conclude that it might as well be. In chapters 5 and 6 Andersen considers implications of his theory for food-web regulation of water quality (i.e. "biomanipulation" or the "trophic cascade") within the context of eutrophication, developing specific predictions for the feasibility of biomanipulation as a function of P loading and lake flushing rate. Remarkably, these predictions, developed from first principles, were accurate regarding the success or failure of six of seven well-documented biomanipulation experiments. Thus, we see it is only a short step to directly apply this theory to questions of considerable human concern.

Andersen's analyses show that, while in ecosystem ecology we have previously considered the primary influence of nutrient limitation on food webs to be in reducing the *quantity* of production available for consumers, a key effect of nutrient limitation on food-web dynamics, as yet largely ignored, may also be in altering the *quality* of that production in stoichiometric terms, with profound

feedbacks to nutrient cycling. Thus, trophic dynamics and nutrient cycling are *not* distinct aspects of ecosystem function. Rather, in Andersen's approach trophic interactions themselves are treated as biogeochemical processes. If this book is unable to put to rest permanently the false dichotomy of "top down" vs. "bottom up" forces in food webs, it will more reflect human affection for simple categories than the state of nature. This book deserves a place on the bookshelf of all aquatic ecologists and indeed contains messages of import for ecologists in general. Even without its key findings, the book would still be useful for its rather amazing compilations

of key ecophysiological parameters for algae and zooplankton. Its synthetic view from physiology to ecosystems makes it an excellent choice for a graduate seminar. Scientists working in any way on aspects of nutrient cycling and(or) trophic dynamics should read this book and then consider whether it is time for a new paradigm.

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